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THE SIGNIFICANCE OF CLUTCH SIZE, EGG COLORATION, AND OTHER
REPRODUCTIVE TRAITS OF MOURNING DOVES

Iowa State University

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The significance of clutch size, egg coloration, and other
reproductive traits of mourning doves

by

David Andrew Westmoreland

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
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DOCTOR OF PHILOSOPHY
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1986

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GENERAL INTRODUCTION

One kind of evidence for the role of natural selection in evolution is that ostensibly maladaptive traits, when examined in the context of a species' natural history, are often found to be adaptive. Pigeons and doves (family Columbidae) have a variety of traits unusual to birds (crop-milk production, exceptionally long breeding seasons, lack of an incubation patch, etc.), and some of these traits seem to be maladaptive. Most birds adjust clutch size in response to food availability (Lack 1947), but columbids lay a small, unvarying number of eggs per clutch. This probably constrains their adaptability to temporal and geographical variation in resources. In addition, columbids build small nests and have conspicuous white eggs, thus predisposing clutches to failure from inclement weather and predation. Despite these traits, the family is successful; columbids are present on every continent (except Antarctica) and almost every major island in the world, and have adapted to habitats ranging from tropical forests to deserts (Goodwin 1983). By conducting field experiments and examining the natural history of mourning doves (Zenaida macroura), I addressed the question, "Why are columbids successful despite their ostensibly maladaptive traits?"

This dissertation is divided into three sections, each of which addresses one or more aspects of columbid

reproduction. In Section I, I show that the seemingly maladaptive traits of mourning doves, and also other unique columbid traits, are actually adaptations that form an efficient reproductive strategy emphasizing production of several broods per nesting season. Section II reports on field experiments that show why mourning doves would not realize an increase in fitness by laying more eggs per clutch. In Section III, I use a simple field experiment to examine the coevolution of egg coloration and constant incubation in doves.

SECTION I. MULTIPLE BROODING AS A REPRODUCTIVE STRATEGY:
TIME-CONSERVING ADAPTATIONS IN MOURNING DOVES

ABSTRACT

Members of the family Columbidae have a reproductive strategy that enables them to proliferate in a variety of habitats throughout the world. For the mourning dove (Zenaida macroura), I identify a suite of adaptations that promotes multiple brooding, a common characteristic among columbids.

Mourning doves are well-adapted for multiple brooding because they produce food (crop milk) for young nestlings in vivo and feed older nestlings a diverse granivorous diet. This facilitates extended breeding seasons and thus multiple brooding. In addition, mourning doves have evolved other traits that enhance the number of broods that can be produced. Small clutch size, constant incubation, fast nestling growth, and fledging at low weight serve to shorten the nesting cycle. Constant incubation may also allow columbids to have no incubation patch. Short nesting cycles also lessen the likelihood of predation at the nest.

Mourning doves also are adapted to renest quickly. By constructing small nests and reusing old nests, they initiate nesting cycles quickly despite their ritualized building behavior. Small clutch size and a lesser role in crop-milk production allow females to initiate new clutches quickly, and sometimes to overlap nesting cycles.

INTRODUCTION

The importance of multiple brooding (i.e., producing two or more clutches per breeding season) as a reproductive tactic has been noted by researchers (e.g., Spencer and Steinhoff 1968, Burley 1980), but the relation between multiple brooding and other life-history traits has received little attention (but see Tinkle 1969, Parmelee and Payne 1973). Among North American birds, the mourning dove (*Zenaida macroura*) is the champion of multiple brooding. Unlike most temperate bird species that attempt one or two clutches per breeding season (Lack 1968), mourning doves often attempt from three to six (Swank 1955, Hanson and Kossack 1963). The species is impressively successful; although the mourning dove is the most frequently harvested game bird in North America (Keeler 1977), both the wintering (Alison 1976) and breeding ranges (Morse 1975) have extended northward in the last few decades. Mourning doves are common breeders in all the contiguous states and parts of Canada, Mexico, and the Caribbean (Goodwin 1983).

Many behavioral and physiological traits of mourning doves can be explained by strong selection for multiple brooding. After briefly reviewing the breeding behavior of mourning doves, I identify a suite of traits that apparently are adaptations for multiple brooding. I focus on a single species for which there is a wealth of ecological and behavioral information, but the proposed "adaptive suite"

(Bartholomew 1972) probably is applicable to pigeons and doves (family Columbidae) in general because members of the group are remarkably alike in breeding behavior (Kendeigh 1952).

Breeding Behavior

Mourning doves are monogamous, and pair bonds at least sometimes persist between nesting seasons (Mackey 1965). Pairs begin courtship in early spring, typically after the male has established a territory containing potential nest sites. During nest building, the male selects twigs and delivers them individually to the female, who arranges them into a small platform (Nice 1922). Pairs often reuse nests, including old nests of other pairs and other species (McClure 1950, Scanlon et al. 1981).

Egg-laying begins 2-3 days after nest initiation. Clutch size is constant at two eggs, and incubation begins after the first is laid (Cowan 1952). Larger clutches of three and four eggs occur about 1% of the time, but probably result from intraspecific nest parasitism (Weeks 1980). Mourning doves incubate constantly, with males sitting from about 1000 to 1800 and females for the remaining hours (Harris et al. 1963, Blockstein 1982). Neither sex develops the vascularized incubation patch typical of other birds (Maridon and Holcomb 1971). The eggs hatch after 13-14 days.

Young mourning doves are fed crop milk, a cheesy conglomeration of epithelial cells sloughed from the crop

mucosa of both parents (Levi 1963). Beginning about the third day after hatching, seeds are mixed with crop milk in gradually increasing proportions; at 6-8 days of age, the young essentially are granivorous (Taylor 1941, Mackey 1954, Laub 1956). The young fledge at about 14 days, but the male continues to feed them for about a week (Hitchcock and Mirarchi 1984).

Mourning doves have one of the longest breeding seasons of all North American birds (Peters 1961); nesting pairs sometimes breed from April through September (McClure 1950, Hanson and Kossack 1963). A single nesting cycle (period from laying first egg to fledging) is 28-30 days; pairs usually attempt to raise multiple broods.

The breeding behavior of mourning doves is typical of columbids. Columbids are monogamous (Delacour 1980), and they build small platform nests (Goodwin 1983). Nest building takes 1-3 days; the interaction between sexes is as previously described (Kendeigh 1952, Goodwin 1983). Clutch size usually is constant for a species, at either one or two eggs. The eggs are small; Rahn et al. (1975) found that columbids produce eggs that are on average less than half the size of those laid by other birds of equal weight. Incubation is continuous, with the exchange between sexes occurring in the morning and late afternoon. Columbids have a bare ventral apterium year-round that does not become vascularized during the breeding season. The length of time

that nestlings are fed crop milk varies among species, but young columbids usually assume the diet of their parents midway through the nestling period. The long breeding season typical of mourning doves has been documented for many columbid species (Frith 1982), and multiple brooding has been reported for many of the species that have been closely studied (e.g., band-tailed pigeons [Columba fasciata], MacGregor and Smith 1955, Gutierrez et al. 1975; rock doves [C. livia], Burley 1980; wood pigeons [C. palumbus], Saari 1979; ruddy ground doves [Columbina talpacoti], Haverschmidt 1953; purple-crowned pigeons [Ducula spilorrhoa], Crome 1975b; Inca doves [Scardafella inca], Johnson 1960; white-winged doves [Zenaida asiatica], Cottam and Trefethen 1968; Galapagos doves [Z. galapagoensis], Grant and Grant 1979). Most columbids that have been bred in captivity produce multiple broods (Delacour 1980, Goodwin 1983).

The family Columbidae is one of the most successful bird taxa; columbids have colonized an array of habitats ranging from jungles to deserts. Of the 284 known columbid species, there are representatives on every continent (except Antarctica) and on every major island in the world (Goodwin 1983). The passenger pigeon (Ectopistes migratorius) was perhaps the most numerous single avian land species of recent times (Schorger 1955).

THE REPRODUCTIVE STRATEGY

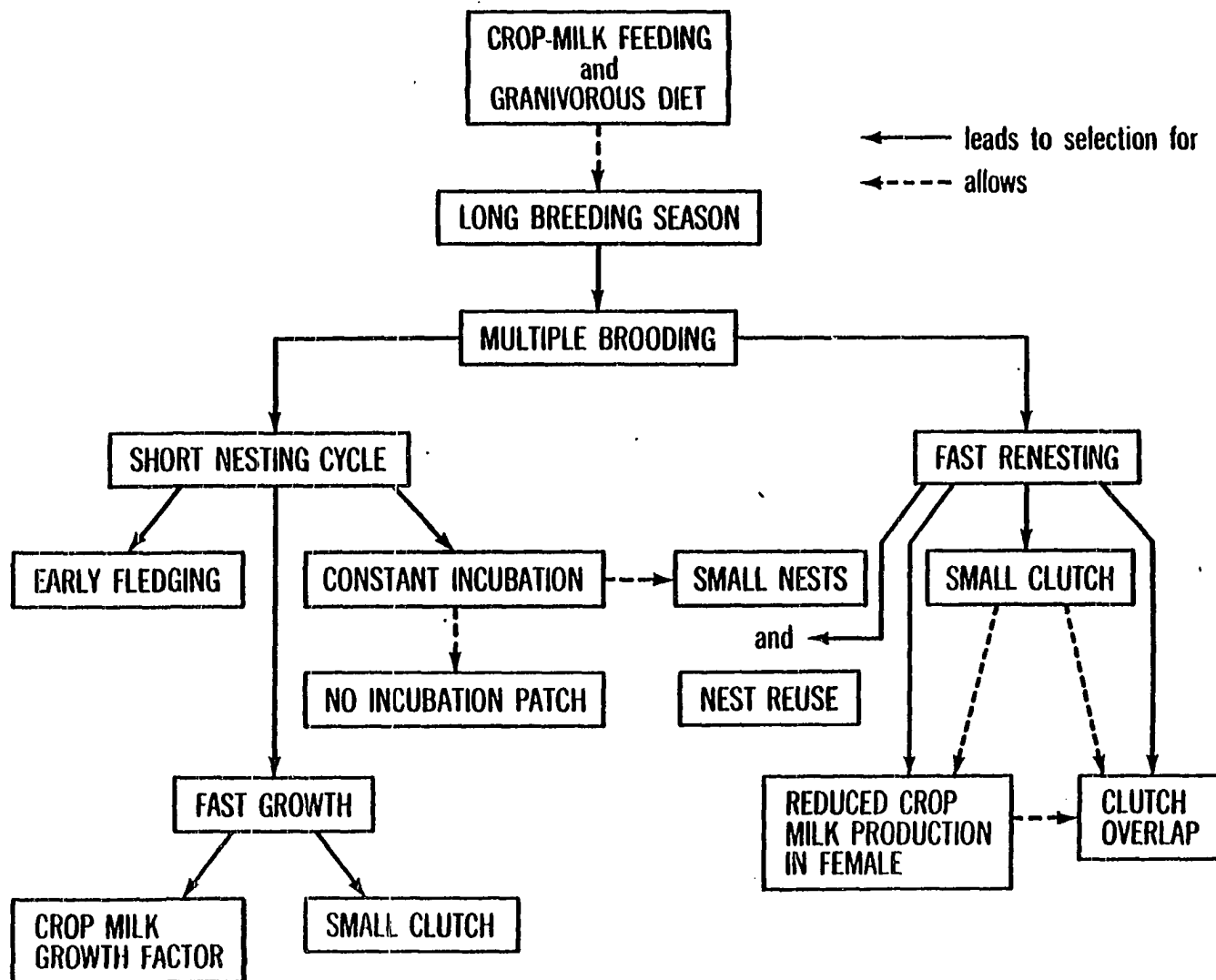
Most birds synchronize reproduction with a brief period of abundant, high-quality food for nestlings (Lack 1950, Skutch 1950, Thompson 1950). But because columbids produce food (crop milk) for young nestlings in vivo and feed older nestlings a diverse diet of seeds (Browning 1959), breeding need not be synchronized with availability of particular foods. The resultant protracted breeding season makes multiple brooding possible.

When multiple brooding strongly affects fitness, the time required to complete nestings is critical. The less time a single nesting takes, the more nestings possible in a breeding season (see also Ricklefs 1984). Columbids could adapt for rapid production of multiple broods by (1) reducing the time interval between successive nesting attempts and (2) reducing the length of the nesting cycle. (I define a nesting cycle as the period from laying the first egg to fledging the last young.) Figure 1 depicts the complex of time-conserving traits that allows mourning doves to accomplish both.

The Nesting Interval

Many researchers have documented the short nesting interval of mourning doves. After a nesting failure, the period until a new clutch is begun ranges from 2 to 25 days, with the most frequent time interval being 6 days in one study (Hanson and Kossack 1963) and 3-5 days in another

Figure 1. Flow diagram outlining the proposed evolution of multiple brooding and associated traits in mourning doves



(Swank 1955). After a successful nesting, mourning doves usually begin a new clutch in 3-6 days (Harris et al. 1963, Caldwell 1964).

Accumulation of nesting material is a slow process for columbids because collecting and exchanging twigs is ritualized, at least partly to enhance gonadogenesis in females (Cheng and Balthazart 1982). Still, mourning doves save time by building small, crudely structured nests. Mourning doves also collect nesting material near the nest site (Cowan 1952, Sayre et al. 1980), which probably serves to ensure males of paternity (see Lumpkin et al. 1982) in addition to saving time and energy. Nests are completed in 2-3 days (Cowan 1952, Goforth and Baskett 1971). Under the constraint of ritualized building, collecting enough twigs to construct a nest comparable to those of other open-nesting birds probably would take mourning doves an additional 4-5 days. Poor nest construction evidently reduces nesting success for mourning doves (Coon et al. 1981), but this negative effect undoubtedly is ameliorated by constant incubation. Koepcke (1972) suggested that small nests are an adaptation for concealment, but this seems unlikely because parents much larger than the nest itself are always present.

By reusing old nests, columbids eliminate the time required for building. For mourning doves, nest reuse often occurs in as many as 35-40% of nesting attempts (McClure 1950, Harris et al. 1963, Scanlon et al. 1981); it does not,

however, ensure better nesting success (Woolfenden and Rohwer 1969, Westmoreland and Best 1985). Thus, it seems plausible that it evolved to save time between nesting cycles.

Crop-milk production is stimulated by secretion of prolactin, which simultaneously suppresses gonadal activity (Bates et al. 1935, 1937). Female mourning doves play a lesser role than males in crop-milk feeding (Blockstein 1982) and reduce crop-milk production 4-6 days before males (Mirarchi and Scanlon 1980). This may allow the antigonadal effect of prolactin to wane, so egg production for the next clutch can begin (Hanson and Kossack 1963). Small clutch size may do the same; by requiring less crop milk, small broods may ameliorate the effect of prolactin in females, thus allowing quick "recycling" of the ovary after the crop-milk phase.

Some individual columbids eliminate nesting intervals altogether by overlapping nesting cycles, i.e., simultaneously caring for two sets of offspring at different stages of development. Small clutch size may facilitate this; the comparatively low energetic cost of producing and feeding only two offspring may enable parents to overlap clutches extensively (Burley 1980). Burley found that experienced captive pigeons care for two sets of offspring (one in the egg stage and the other as nestlings) 70% of the time. Captive (Hanson and Kossack 1963) and wild (Mark Sayre, Department of Forestry and Wildlife Management,

University of Massachusetts, pers. comm.) mourning doves sometimes overlap clutches by 14% or more by laying eggs when the young of the previous nest are 10 or 11 days old. There is also circumstantial evidence for overlap in wild wood pigeons and stock doves (Columba oenas) (Murton and Isaacson 1962).

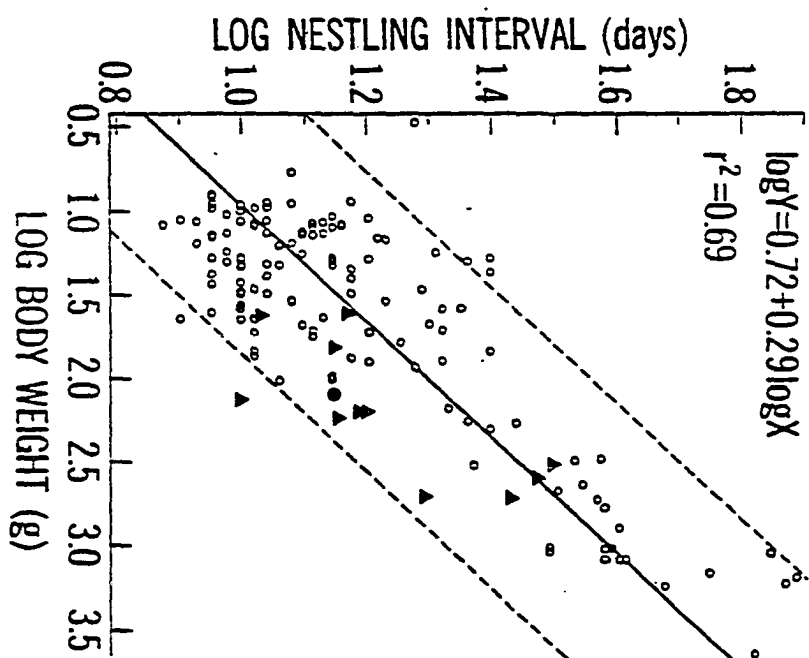
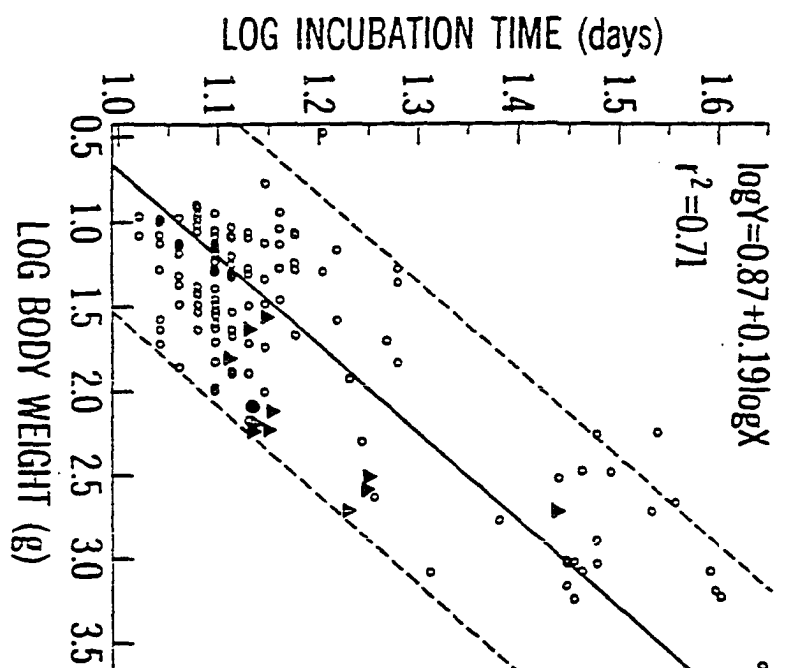
The Nesting Cycle

If columbids are strongly selected to have short nesting cycles (Figure 1), the trend should be apparent when they are compared with other birds. To examine this, I regressed the time required for incubation and nestling growth to fledging on body weights for 128 altricial species of open-nesting land birds (Figure 2). Incubation and nestling times were taken from Harrison (1978) and body weights from sources in the Auk, Condor, Wilson Bulletin, etc. (data and references available from author).

Examination of Figure 2 reveals that columbids save time in both the incubation and nestling stages. Overall, columbid nesting cycles are 22% shorter than those predicted by the regression line. Only one value for columbids lies outside the 95% confidence interval, but 11 of 12 and 10 of 11 of the incubation and nestling intervals, respectively, fall below the regression lines. The probability of this occurring by chance alone in either case is < 0.01 (sign test, Gibbons 1976).

Several traits of mourning doves may serve to shorten

Figure 2. Relationship between body weight and incubation or nestling interval for 128 species of altricial, open-nesting land birds. The regression line was calculated for noncolumbids (open circles). Triangles represent columbids, and the closed circle represents the mourning dove. Dashed lines show the 95% confidence intervals for predicted values



incubation time. Small egg size undoubtedly has a strong influence; Rahn and Ar (1974) showed the positive correlation between incubation time and egg weight. However, constant incubation probably also plays a role. Mourning dove eggs and nestlings less than 6 days old essentially are ectothermic (Breitenbach and Baskett 1967). In general, bird eggs cool rapidly when parents are absent and rewarm slowly after their return (Drent 1972). Boersma and Wheelwright (1979) found that the incubation period of fork-tailed storm petrels (Oceanodroma furcata) increases in direct relation to the amount of time spent away from the nest. Most birds take respites from incubation, usually to forage (Skutch 1962, Ricklefs 1974, Drent 1975). Columbids store large quantities of food in their crops, so incubation is not interrupted by a need for food. The constant source of heat supplied from laying until late nestling growth ensures that offspring development is continuous. Through constant nest attentiveness, mourning doves, ring doves (Streptopelia risoria), and white-winged doves can maintain their eggs at viable temperatures even during extreme heat (Russell 1969, Walsberg and Voss-Roberts 1983).

Constant incubation may have also eliminated the need for vascularized incubation patches in columbids. According to Ackerman and Seagrave (1984), incubation patches in birds transfer little heat with eggs during the steady-state conditions that occur when eggs are continuously covered.

Thus, for columbids, development of incubation patches would be unnecessary. Constant incubation also may have led to the evolution of white (noncryptic) egg coloration in columbids. However, other evidence (Section III) suggests that cryptic coloration may result in higher hatching success even when eggs are incubated continuously.

Columbids are an exception to the general rule that nestlings of species with small clutches have slow growth rates (Ricklefs 1968b); columbid growth rates are comparable to, if not faster than, those of raptors and passerines. Their method of feeding young may be the reason. Crop milk is high-quality food for nestlings, being composed of 65-81% water, 13-19% protein, 7-13% fat, and 1.5% ash (Needham 1942). But it also contains an unidentified factor that promotes fast growth. Pace et al. (1952) compared growth rates of White-rock (Gallus gallus) chicks fed ad libitum on chick ration with those of chicks whose diet was supplemented with small amounts (5 g/day) of Rock Dove crop milk. Although crop milk was fed for only 6 days after hatching, treatment chicks grew significantly (t-test for slopes, $P < 0.001$, analysis mine) faster than controls until the experiment ended when chicks were 42 days old. Evidently, crop milk stimulated chicks to eat more ration.

Some young columbids feather quickly and leave the nest at relatively low weight. For 94 altricial, noncolumbid species, Ricklefs (1968b) found that the ratio of fledging

weight to adult weight ranged from 0.62 to 1.45; for seven of eight columbid species (Table 1), the ratio ranges from 0.25 to 0.66. In concert with fast growth, early fledging must significantly shorten the nestling period. After leaving the nest, young mourning doves usually become independent in 4-7 days (Hitchcock and Mirarchi 1984). Admittedly, my comparison of nesting cycle lengths would be more reliable if I included this period, but there are few published data on the postfledging period of columbids or noncolumbids.

Small clutches also may be an adaptation for a short nesting cycle. Mourning dove eggs usually are laid on alternate days (Hanson and Kossack 1963), so increasing clutch size to three would have a direct, although minor, effect on the duration of the nesting cycle. A larger clutch also may prolong the incubation period, as Zimmerman (1983) found with dickcissels (Spiza americana). During the early nestling stage, parents with a given amount of crop milk may raise a small brood quickly or a large brood slowly (Lack 1968). Some evidence suggests, however, that some individual columbids may simply increase crop-milk production for a larger brood. Murton et al. (1963) found that adding a third nestling to some wood pigeon nests had no effect on growth during the crop-milk stage. This is not true, however, for other wood pigeons (Murton et al. 1974), feral pigeons (Burley 1980) or mourning doves (Section II). After the crop-milk phase, nestling growth may be limited by the rate

Table 1. Fledging weight:adult weight ratios for columbids

| Species | Weight (g) | | Ratio |
|------------------------------|----------------------|---------|-------|
| | Fledging | Adult | |
| <u>Columba livia</u> | 352 (8) ^a | 313 (8) | 1.13 |
| <u>C. palumbus</u> | 277 (3) | 500 (9) | 0.55 |
| <u>Columbina talpacoti</u> | 28 (2) | 45 (2) | 0.62 |
| <u>Ducula spilorrhea</u> | 260 (5) | 500 (5) | 0.52 |
| <u>Ptilinopus superbus</u> | 30 (6) | 120 (5) | 0.25 |
| <u>Streptopelia decaocto</u> | 70 (7) | 145 (7) | 0.48 |
| <u>Zenaida asiatica</u> | 113 (4) ^b | 170 (4) | 0.66 |
| <u>Z. macroura</u> | 72 (1) | 115 (1) | 0.63 |

^aSources: (1) McClure 1941, (2) Haverschmidt 1953, (3) Murton et al. 1963, (4) Cottam and Trefethen 1968, (5) Crome 1975a, (6) Crome 1975b, (7) Rana 1975, (8) Burley 1980, (9) R. A. Ackerman, Department of Zoology, Iowa State University, pers. commun.

^bEstimated from linear extrapolation of the growth-rate curve.

at which the parents gather seeds. Haas (1980) found that mourning dove nestlings attended by a single parent after the crop-milk phase take up to 3.8 days longer than normal to fledge. He did not, however, report fledging weights. Murton et al. (1974) studied the effects of brood size on growth rates of nestling wood pigeons, a species that normally lays two eggs. They found that nestlings in broods of three grew slower than those in broods of two, but parents of three-young broods nevertheless were often successful in fledging the young. Band recoveries within 1 month of fledging indicated that young from broods of three had lower survival, but the difference was not statistically significant. Section II further addresses the question of whether or not small clutch size is an adaptation for short nesting cycles.

The Importance of Predation

Adaptations that shorten the nesting cycle also are advantageous in reducing the probability of predation. When the nesting cycle is short (i.e., there are fewer days of nest exposure), there is less chance of a nest being discovered by a predator (see Mayfield 1975). Also, the loss of a small clutch represents less wasted parental investment. Predation-related advantages undoubtedly contribute to the success of the columbid reproductive strategy, but clutch overlap and reuse of nests built by other individuals or other species cannot be explained as adaptations for predator

avoidance. Also, this proposed suite of adaptations is relatively ineffective at reducing losses to predation. From Ricklefs' (1969: 12) data on daily nest failure, the mean rate for mourning doves is about the same as that for the 15 other open-nesting, altricial species listed (2.1% vs. 2.4%, respectively, Student's t-test, $P = 0.38$). Thus, I believe that predation probably is of secondary importance in the evolution of the columbid reproductive strategy.

SECTION II. WHY DO MOURNING DOVES LAY ONLY TWO EGGS?

ABSTRACT

To examine factors possibly limiting clutch size for mourning doves (Zenaida macroura), I exchanged eggs of equal age among nests to create clutches of one and three eggs in addition to natural, two-egg clutches. Adults were fully capable of incubating three-egg clutches and brooding three nestlings at normal temperatures. Nestlings in enlarged broods grew slower than those in control (two-young) broods during the crop-milk stage, and generally had less full crops throughout the nestling period. Enlarged broods took 1.3 days longer to fledge and fledged with normal carpometacarpus lengths but at 83% normal fledging weight. Parents of enlarged broods fledged an estimated 23% more offspring than those of control broods. However, low postfledging survival probably negates the advantage to parents rearing three offspring per nest.

INTRODUCTION

Since Lack's (1947, 1948) classic treatise on the significance of clutch size in birds, the topic has received considerable theoretical (e.g., Cody 1966, Charnoy and Krebs 1974, Foster 1974, Brockelman 1975) and empirical (e.g., Ricklefs 1968b, Safriel 1975, Crossner 1977, Haymes and Morris 1977, Greenlaw 1978) attention. Lack (1947) contended that nidicolous birds raise as many young per nest as possible within the constraint of local food supply. As food abundance varies, clutch size should vary accordingly. This idea has been supported by some studies (Plumb 1965, Lloyd 1977) and rejected in others (Vermeer 1963, Harris 1970). Cody (1966) suggested that clutch size is the outcome of competing demands on the energy budgets of breeding individuals. He hypothesized that clutch sizes would be lower in stable climates where predation avoidance and competition assume increased importance and require a greater proportion of the energy budgets of parents. Cody used this concept to explain geographical trends in clutch size of avian communities, but it has not been tested for individual species.

On the basis of either Lack's or Cody's hypothesis, the clutch size of granivorous pigeons and doves (family Columbidae: subfamily Columbinae) is enigmatic; these species virtually always lay two eggs (Goodwin 1983) despite regional and temporal variation in resource abundance or effects of

competing energy demands. Yet, the group as a whole is successful; columbids occupy habitats from jungles to deserts, and there are representatives on every continent (except Antarctica) and every major island in the world (Goodwin 1983).

By manipulating clutches, I tested several possible limitations on clutch size of the mourning dove (Zenaida macroura), a typical columbid widely distributed in North America (Goodwin 1983). Specifically, I addressed four hypotheses: First, clutch size may be limited by the inability of parents to incubate three eggs and/or brood three nestlings. This seems likely because columbids, unlike most other birds, do not have vascularized brood patches (Jones 1971, Maridon and Holcomb 1971), and they build small, poorly insulated nests (Ricklefs 1974). Second, clutch size may be limited because adults cannot produce an adequate supply of crop milk for three young. Nestlings are fed crop milk for the first 5-7 days of life (Taylor 1941, Laub 1956). Third, clutch size could be curtailed by the inability of parents to gather enough seeds for nestlings after the crop-milk period. Finally, clutch size in columbids may be a compromise between the risk of predation and the maximum number of young that can be reared (sensu Lack 1948). Nestlings in large broods may grow slower and stay in the nest longer, thus increasing the likelihood of the nest being discovered by a predator.

METHODS

Field work began in early May and continued through August 1984-1985 at Big Creek State Park in central Iowa. The park contains several km of coniferous trees planted in linear rows as windbreaks in addition to perennially weedy areas, both of which are used as nesting sites by doves.

I searched windbreaks at least once every two weeks. When a nest was discovered, I recorded light intensity (as a percentage of ambient light intensity), the amount of cover around the nest, distance from the nest to the top of the tree, and nest width. Westmoreland and Best (1985) found that these features are related to nesting outcome; details of how they were measured can be found therein. Each clutch was aged by candling (Hanson and Kossack 1963). I created experimental clutch sizes of one and three eggs by randomly exchanging eggs of equal age between nests; some nests (controls) were not manipulated. The egg exchanges were done as soon after nests were discovered as possible. Some nests were found after hatching, however, and these were added to the control treatment. To minimize predation losses, nests were visited infrequently or not at all during incubation.

In 1985, I installed camouflaged, wire-mesh nesting cones under each nest that successfully hatched, in order to stop nestlings from falling or being pushed from nests. I removed the nest while wiring the cone to branches, and then placed the nest and nestlings securely in the center of the

cone. Cones were about 25 cm in diameter, considerably increasing the surface area of nests.

After hatching, nestlings were individually marked with ink spots on their bellies and were visited at 2-3 day intervals until they were 10 days old. Most visits were between 1000 and 1400. At each visit, nestlings were weighed to the nearest 0.5 g, gular temperatures were measured with a digital thermometer, and carpometacarpus length (CL) was recorded. CL was measured from the bend of the wing to the distal tip of soft tissue; I did not include the length of feathers in this measure. I also palpated crops to determine fullness (0--empty to 4--full). Nestlings older than 10 days tend to fledge when approached closely. To determine the length of the nesting cycle, therefore, I checked with binoculars for the presence of such nestlings each day until they fledged.

Growth curves were fitted to the logistic equation by using the nonlinear analysis program of SAS (Helwig and Council 1979). Growth-rate constants, inflection points, and slopes and intercepts of regression lines were compared using z-tests. Nestling ages, weights, temperatures, CLs, and crop fullnesses were averaged when more than one nestling was present in a nest because each brood was considered an experimental unit. When partial failure (i.e., death of some, but not all nestlings) occurred in a brood, I used only the data collected before the loss. Nest success was

calculated by the Mayfield (1975) method, and evaluated by using two-tailed tests with a significance level of $P < 0.1$ (Hensler and Nichols 1981). A significance level of $P < 0.05$ was used for all other statistical tests.

RESULTS

Of the 292 nests I found, 27 were abandoned and 14 were eliminated for various reasons (research-related nest failure, eggs collected for other purposes, etc.), leaving 251 nests for analyses. Nest-site features did not differ significantly among treatments, so it is unlikely that nest placement influenced treatment differences (Table 1).

Ability to Incubate Eggs

All fertile eggs not eaten by predators hatched successfully, regardless of clutch size. The length of incubation did not differ among treatments (Table 2), but I usually did not exchange eggs between nests until midway through the incubation period.

Ability to Brood and Feed Nestlings

Growth rates

Both body weight and CL were indices of nestling growth, and the two variables were strongly correlated ($r = 0.95$, $N = 510$). Nestling weight had greater coefficients of variation than CL, probably because of variation in the amount of food in nestlings' crops. Therefore, I used CL as a measure of growth in most analyses.

Growth rates were inversely related to brood size (Figure 1, Table 3), and growth was significantly slower for enlarged broods than for other brood sizes. The slow growth of enlarged broods occurred primarily during the crop-milk phase. Nestlings in enlarged broods seemed to compensate for

Table 1. Values (mean \pm s.e.) of nest-site features for each clutch-size treatment^a

| Variable | Clutch/Brood Size | | |
|---------------------------------------|-------------------|----------------|----------------|
| | 1 (N=80) | 2 (N=103) | 3 (N=68) |
| Substrate height above nest level (m) | 1.9 \pm 0.1 | 2.1 \pm 0.2 | 2.3 \pm 0.1 |
| Relative light intensity (%) | 15.9 \pm 1.3 | 17.1 \pm 1.2 | 17.7 \pm 1.6 |
| Concealment | 2.2 \pm 0.1 | 2.2 \pm 0.1 | 2.3 \pm 0.1 |
| Nest width (mm) ^b | 116 \pm 1.5 | 116 \pm 1.2 | 118 \pm 1.9 |

^aNo differences among treatments are significant.

^bDoes not include 27 nests built by other species but reused by mourning doves.

Table 2. Lengths of egg-laying, incubation, and nestling periods for treatments of one, two, or three eggs/nestlings^a

| Treatment | Length of period (days) | | |
|-----------|--------------------------------|------------------------|------------------------|
| | Egg-laying ^b (N) | Incubation (N) | Nestling period (N) |
| 1 | 0 | 13.9 ± 0.09 A (48), | 11.8 ± 0.33 A (31) |
| 2 | 1.5 | 13.8 ± 0.11 A (53) | 12.6 ± 0.47 A (25) |
| 3 | 3.0 | 14.0 ± 0.08 A (42) | 13.9 ± 0.15 B (15) |

^aValues with the same letter within a column are not significantly different (multiple range test).

^bHanson and Kossack (1967) estimate a laying interval of 1.5 days for mourning doves.

Figure 1. Growth of nestling mourning doves in broods of one, two, or three nestlings. Vertical bars represent 95% confidence intervals for mean values, and arrows indicate the inflection points of the curves.

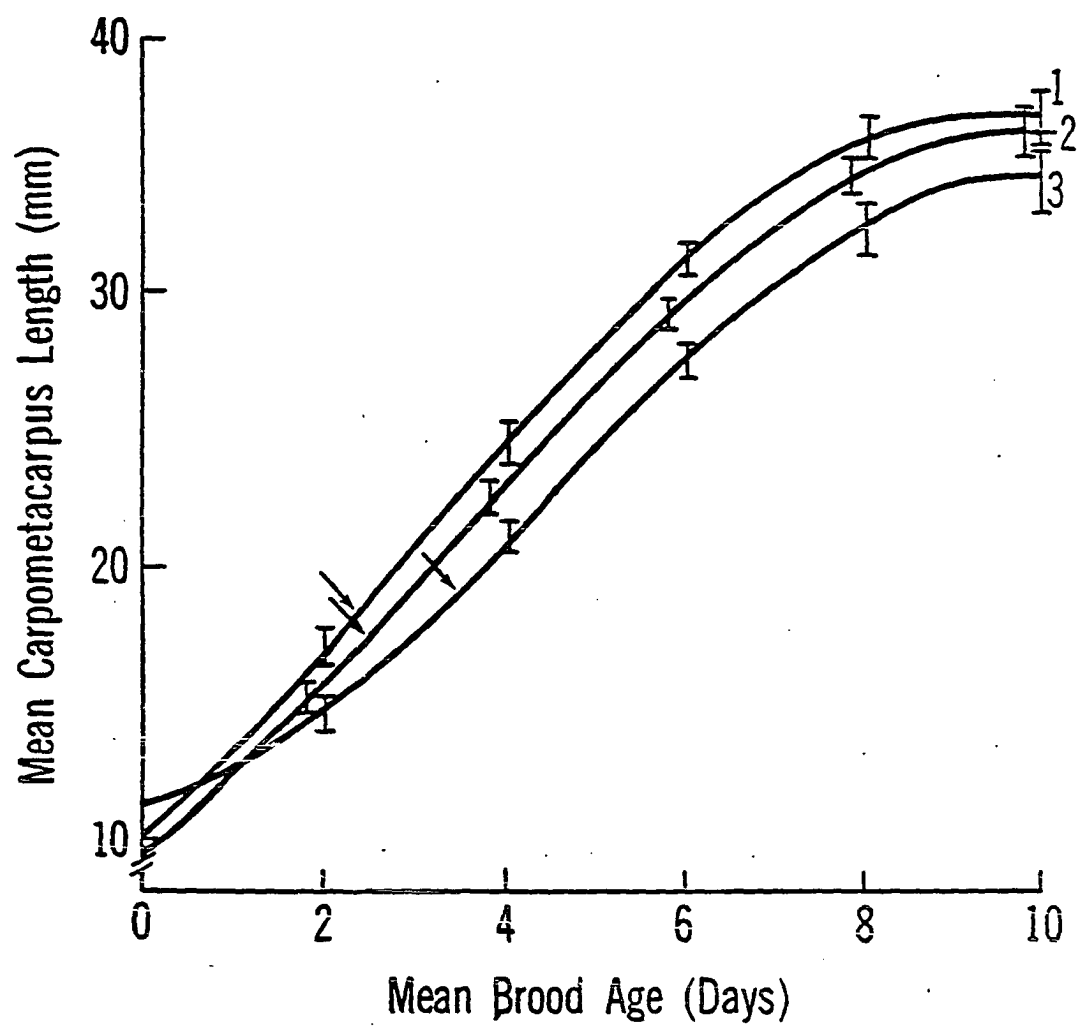


Table 3. Growth parameters and fledging sizes as estimated by logistic equations for mourning dove broods of one, two, or three nestlings^a

| Brood Size | Growth-rate Constants for each period ^b | | | Fledging Size | |
|----------------------------------|--|--------------------|----------------------|----------------------|-------------------------|
| | Crop-milk | Granivorous | Entire period | CL (mm) ^b | Weight (g) ^c |
| 1 | 0.327 ± 0.054^d A | 0.010 ± 1.84 A | 0.427 ± 0.027 A | 37 | 66 |
| 2 | 0.346 ± 0.050 A | 0.100 ± 0.34 A | 0.405 ± 0.022 A | 37 | 63 |
| 3 | 0.200 ± 0.044 B | 0.632 ± 0.48 A | 0.294 ± 0.021 B | 38 | 52 |
| Successful broods of three | 0.233 ± 0.081 AB | 0.688 ± 0.63 A | 0.359 ± 0.035 AB | 36 ^e | 51 ^e |

^aValues with the same letter within a column are not significantly different.

^bThese parameters based on equations derived for CL growth (see text).

^cEstimates based on equations derived for increase in weight as nestlings aged.

^dAsymptotic standard error (Galant 1975).

^eEstimates for a nestling period of 13.9 days (see text).

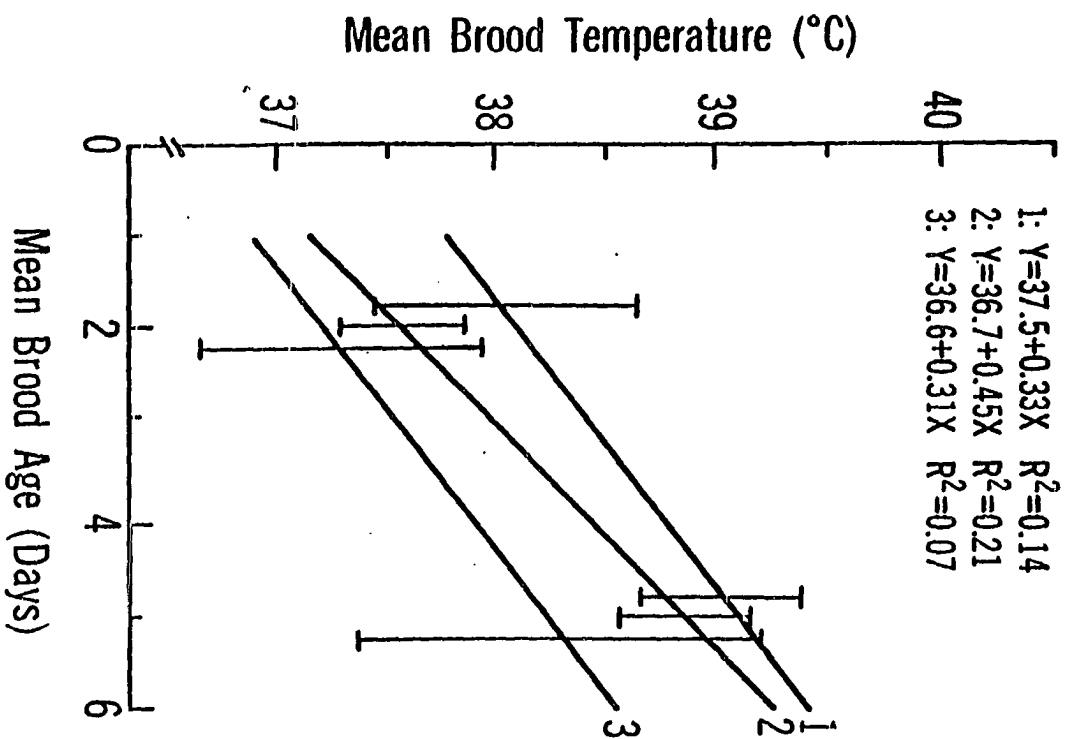
slow early growth by growing faster than other broods during the granivorous phase. The differences among growth rates during this period were not significant, however, probably because of the large variance in growth rates for all three brood sizes. The significantly later inflection point of the growth curve for enlarged broods also reflects a maximum growth rate later in the nestling period.

Nestling periods differed significantly among treatments, with enlarged broods taking about 1.3 days longer to fledge than control broods (Table 2). Using the growth-rate equations derived for each treatment, I estimated the size of young at fledging. Nestlings from enlarged broods fledged with CLs comparable to those of control broods, but at only about 83% of control-brood fledging weight (Table 3).

Brood temperatures

Because mourning dove nestlings less than 6 days old have not fully developed the ability to thermoregulate (Breitenbach and Baskett 1967), hypothermia could account for the slow growth of enlarged broods. To examine the importance of parental brooding, I regressed nestling temperature on age during this period for each treatment. The resulting relationships were weak but significant (slopes > 0 , $P < 0.05$) or nearly so ($P < 0.1$) for all three treatments; mean brood temperature increased as nestlings aged (Figure 2). Single nestlings were slightly warmer than

Figure 2. Relationship between mean gular temperature and mean age for mourning dove broods of different size. Neither slopes nor intercepts differ significantly among treatments. Vertical bars represent 95% confidence intervals for mean values.



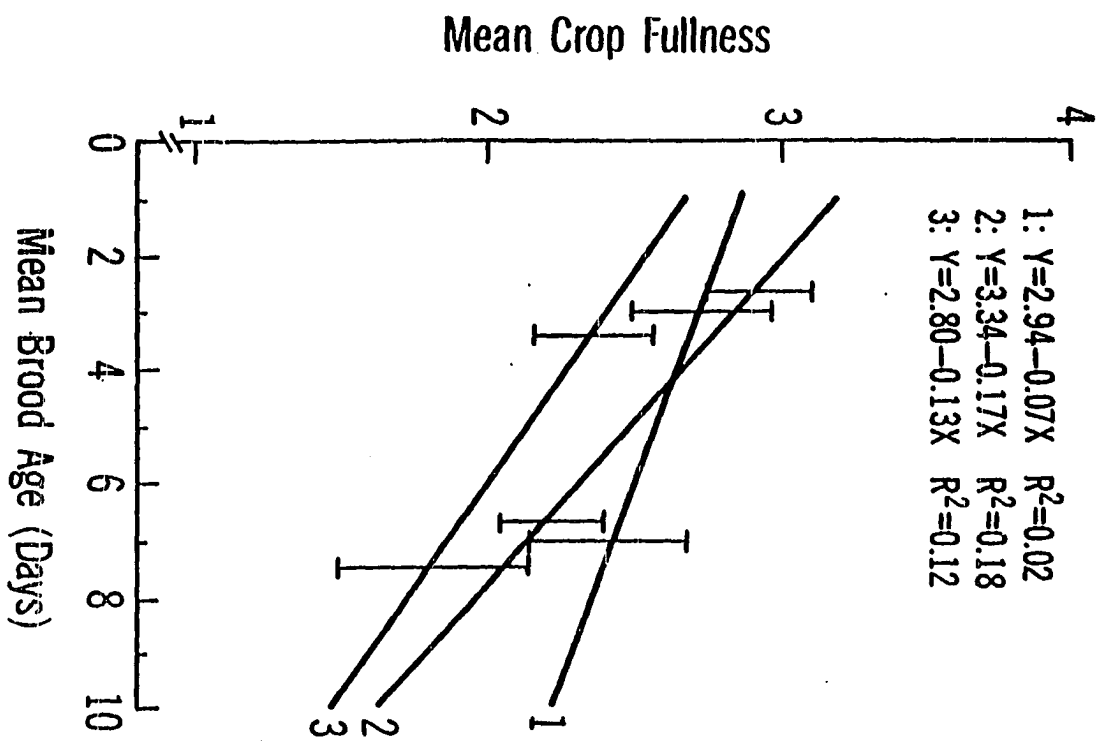
nestlings in other treatments, but differences were not significant. There was no treatment x age interaction, i.e., a significant difference in brood temperatures among treatments did not become evident as nestlings aged. Therefore, it seems unlikely that the lack of a brood patch in parents prevented adequate brooding of enlarged broods.

Crop fullness

Crop fullness was inversely related to nestling age in all three treatments (Figure 3), probably because parents were unable to fill the growing crops. The decrease in fullness occurred at a significantly lower rate for lone nestlings than for nestlings in other treatments. The intercepts of regression lines differed significantly between control and enlarged broods, i.e., nestlings in enlarged broods generally had less in their crops than those in control broods.

Starvation or sibling competition resulted in partial nest failures in 17 (37%) three-young nests, but in only four (5%) two-young nests. In 1984, before I reinforced nests with metal cones, nestlings were sometimes found dead or moribund beneath nests. Because they often had food in their crops, I surmised that they died of exposure rather than starvation. Nestlings may have been pushed from nests during feeding bouts, as siblings flap their wings vigorously when begging. In 1985, nestlings usually died without falling from the reinforced nests; they appeared to have been crushed

Figure 3. Relationship between fullness of nestling crops and mean ages for broods of one, two, or three mourning doves. The intercept for two-nestling broods was significantly greater than that for three-nestling broods; the regression for broods of one nestling had a significantly greater slope than those of larger broods. Vertical bars represent 95% confidence intervals for mean values.



by siblings or to have starved.

Growth of successful, enlarged broods

For any factor to effectively curtail the evolution of larger clutch size in columbids, it must affect all breeding pairs. Some mourning dove pairs inherently may be able to raise enlarged broods whereas others may not. To test this, I compared growth of the 15 enlarged broods that did not suffer partial failure (representing pairs seemingly better at rearing enlarged broods) to growth of control broods. The treatments did not differ significantly in inflection points, but the difference in growth-rate constants was nearly significant ($P = 0.1$, Table 3). The intercept of the regression line of crop fullness on nestling age for successful enlarged broods ($Y = 2.8 - 0.12X$, $R = 0.32$) was significantly lower than that for control broods (Figure 3). Thus, parents of successful enlarged broods did not feed their nestlings enough to allow growth equal to that of two-nestling broods.

Clutch Size and the Risk of Predation

Daily survival probabilities (based on failures of entire clutches) did not differ significantly among treatments (Table 4), but the disparity between success of control and manipulated clutches approached significance ($P = 0.14$). After we manipulated clutches, both sexes continued to exchange nest duties at the normal time intervals (Harris et al. 1963, Blockstein 1982), so the frequency of flights to

Table 4. Nesting success estimates based on daily survival probabilities (DSP) for each treatment^a

| Nest stage | # of nests | # of failures | DSP \pm SE | Estimated success (%) ^b |
|-----------------|------------|---------------|-------------------|------------------------------------|
| Incubation | | | | |
| One egg | 61 | 16 | 0.951 ± 0.012 | 50 |
| Two eggs | 89 | 33 | 0.931 ± 0.012 | 37 |
| Three eggs | 57 | 19 | 0.942 ± 0.013 | 43 |
| Nestling period | | | | |
| One nestling | 60 | 21 | 0.960 ± 0.009 | 57 |
| Two nestlings | 74 | 31 | 0.954 ± 0.008 | 52 |
| Three nestlings | 49 | 17 | 0.969 ± 0.008 | 64 |
| Combined | | | | |
| Treatment 1 | 76 | 37 | 0.957 ± 0.007 | 28 |
| Treatment 2 | 108 | 64 | 0.945 ± 0.007 | 20 |
| Treatment 3 | 67 | 36 | 0.959 ± 0.007 | 31 |

^aNo differences among treatments are significant.

^bBased on incubation and nestling periods of 14 days each.

and from the nest did not differ among treatments. Researcher disturbance could have biased these estimates of daily survival probabilities (Westmoreland and Best 1985); therefore, we evaluated nesting success assuming no differences in daily survival probabilities among treatments. Mayfield (1975) estimates of nesting success were calculated for each treatment by using the daily survival probabilities of 0.966 for egg-laying and incubation and 0.947 for the nestling period. These survival probabilities were reported by Westmoreland and Best (1985) for unvisited mourning dove nests. The egg-laying and nestling periods presented in Table 2 were used in comparing the three treatments.

Nests with longer nest-cycles, and thus a greater chance of being discovered by predators, have lower probabilities of success. Probabilities of nest success were 0.32 for single-nestling broods, 0.30 for control broods, and 0.26 for enlarged broods. The estimated number of young fledged per nesting attempt was 0.32, 0.60, or 0.78 for parents raising broods of one, two, or three nestlings, respectively. Thus, parents of enlarged broods would be expected to fledge 23% more young per nesting attempt than parents of control broods.

DISCUSSION

I can reject two of the hypothesized limitations to clutch size for columbids. Adults provided adequate heat for enlarged clutches/broods and fed nestlings enough seeds to allow normal growth during the later stages of nestling development. Limited crop-milk production, the risk of predation, and other constraints probably interact in limiting clutch size of mourning doves.

Ability to Feed Nestlings

The crop-milk phase seems to be the period that imposes the strongest physiological limit to clutch size for mourning doves. Burley (1980) manipulated brood sizes of captive rock doves (Columba livia) and identified the crop-milk stage as the period of greatest parental demand. Likewise, Haas (1980) found that mourning dove nestlings usually die when one parent is killed during the crop-milk period, but survive to fledge if the parent is killed later.

Limits to the rate of crop-milk production may explain the surprising constancy of clutch size in columbids. Most birds seem to adjust clutch size in response to fluctuations in local food availability (Lack 1947). Mourning doves range across North America and breed in habitats from deserts to forests, yet more than 99% of their clutches contain two eggs (Weeks 1980). If maximum crop-milk production is regulated by rates of physiological processes involved in its formation (e.g., mitosis, prolactin production, deposition of lipids in

the nutritive epithelium, etc.) and not by resource abundance, clutch size would not vary. Some evidence suggests that columbid parents require a relatively small increase in food intake during crop-milk production. Brisbin (1969) found that, during the crop-milk phase, caloric intake of captive ring doves (Streptopelia risoria) fed ad libitum increases by about 30% above nonbreeding intake while fat indices remain constant. In comparison, most birds when breeding maintain metabolic rates 2.4 - 4 times higher than their basal metabolic rates (Utter and Lefebvre 1973, King 1974, Gaston 1985).

Limited crop-milk production evidently sets an upper limit to clutch size for mourning doves, but it does not restrict them to a brood size of two nestlings. Among nests undiscovered by predators in this study, half of the adult pairs given an additional nestling successfully fledged all three young. But nestlings in enlarged broods sacrificed weight gain (perhaps fat deposition) for skeletal (CL) growth and fledged at lower weight than control nestlings. Murton et al. (1974) and Burley (1980) also found that columbid nestlings in experimentally enlarged broods fledge at low weight.

Clutch Size and the Risk of Predation

One might expect that parents rearing three young would benefit from a 50% greater enhancement of fitness than those rearing two young. The longer nesting cycle of enlarged

broods reduced, but did not negate, this potential increase (assuming no differences in nest success among treatments). The findings of Murton et al. (1974) and Burley (1980) also suggest an increase in fitness for columbid parents with enlarged broods. If it is advantageous for columbids to rear more young, why don't they? The reason probably is that other factors reduce fitness for parents of enlarged broods or otherwise constrain the evolution of larger clutches.

Other Constraints

Postfledging survival

The seeming advantage to rearing three-young broods could be reduced if underweight fledglings have low survival. Fledgling mourning doves are gradually weaned from the parents during a two-week, postfledging period (Hitchcock and Mirarchi 1984), when survival is surprisingly high (Grand et al. 1984). I used Grand et al.'s percent mortality data to calculate a daily survival probability of 0.992 for normal fledglings during this period. If fledglings from enlarged broods had daily survival probabilities of 0.974 or less, the potential increase in fitness for adults raising them would be negated. This difference in survival between fledglings from control versus enlarged broods is well within that reported for wood pigeons (Columba palumbus). Murton et al. (1974) found that survival of fledglings from enlarged broods was 44% of that for control fledglings during a 1-month, postfledging period.

Extended nesting intervals

Underweight fledglings may require a longer period of postfledging parental care, resulting in a longer interval between successive nesting attempts. This could lower the fitness of adults by reducing the number of nesting cycles possible in a season (Section I). I followed one color-marked pair of adults through four nesting cycles and monitored renesting intervals after they raised broods of one, two, and three nestlings. The adults renested 4 days after the young fledged, regardless of the previous brood size. After a successful nesting, mourning doves usually begin a new clutch in 3-6 days (Harris et al. 1963, Caldwell 1964). These meager findings do not suggest a longer nesting interval for pairs raising enlarged broods, but such a relationship has been reported for house sparrows (Passer domesticus; McGillivray 1983).

Small nest size

Survival of mourning dove nestlings may be curtailed by the small size of nests. I found that nestlings in enlarged broods often fell from nests not reinforced with cones. The size of mourning dove nests varies greatly, however, because they reuse nests built by other species (e.g., McClure 1950, Scanlon et al. 1981, Westmoreland and Best 1985). If selection favored an increase in clutch size, it seems likely that mourning doves could adapt to build larger nests or use other species' nests more frequently.

Costs of oogenesis

Finally, clutch size in columbids might be constrained by a factor that I could not measure--the cost of oogenesis. It seems unlikely that producing a clutch is energetically expensive to columbid females, however, because both the eggs and clutches are small. Rahn et al. (1975) found that columbids produce eggs that are on average less than half the size of those laid by other birds of equal weight. I (Department of Animal Ecology, Iowa State University, unpubl. data) examined the relationship between body weight and the total energy content (kcal/g x egg weight x clutch size) of clutches for 23 altricial, terrestrial bird species. Compared to mourning doves, noncolumbids of comparable weight invest 2.5 times more energy in a clutch (15.9 vs 40.3 kcal). Thus, it seems unlikely that the clutch size of mourning doves is constrained by the cost of producing eggs.

SECTION III. THE COEVOLUTION OF EGG COLORATION AND
INCUBATION CONTINUITY IN MOURNING DOVES

ABSTRACT

I studied the adaptive value of cryptic egg coloration by comparing the daily survival probability of natural (white) mourning dove (Zenaida macroura) clutches to that of clutches spattered with brown tempera paint (simulating cryptic coloration). Cryptic clutches had significantly greater survival probabilities in nests where incubation was interrupted (i.e., parents were sometimes away from the nest) but did not have significantly higher survival in continuously incubated nests.

I argue that white egg coloration in pigeons and doves was a selective pressure for development of continuous incubation. Other birds that lay white eggs in open nests often have similar adaptations.

INTRODUCTION

The color of birds' eggs varies greatly; some species lay white eggs, whereas others lay eggs with intricate color patterns. Researchers have proposed two primary functions of egg coloration. When in direct sunlight, uniformly light-colored eggs are less likely to overheat than darker eggs (Montevecchi 1976a) because light colors generally reflect solar radiation more efficiently. In contrast, scattered dark spots or scrawls probably benefit eggs by making them less visible to predators (Lack 1958). Montevecchi (1976a) suggested that these functions of egg coloration are opposing selective forces, although Bakken et al. (1978) found that the particular pigments used for cryptic coloration minimize heat absorption from direct insolation.

Surprisingly little research has been done to document the effectiveness of cryptic egg coloration. Tinbergen et al. (1962) and Montevecchi (1976a) placed cryptic and white eggs in meadows visited by avian predators and found that cryptic eggs suffered less predation. Bertram and Burger (1981) had similar results when they placed white vs. brown Ostrich (Struthio camelus) eggs on bare ground. In contrast, Kruijt (1958) found that egg speckling did not reduce predation by Herring Gulls (Larus argentatus) on artificial nests. These studies were simplistic because eggs in nature are placed in specific microhabitats (nest sites) and are, to

some extent, protected by parents. Here, I report the results of a study on the effects of egg crypticity involving nests with parents actively attending them.

Pigeons and doves (family Columbidae) are unusual among open-nesting birds because they lay relatively conspicuous eggs of a uniform white or buff color. Columbids parents incubate continuously (Kendeigh 1952), so selective pressure for egg crypticity probably is weak. White eggs and constant incubation make columbids ideal for studies of egg coloration because a researcher can control both egg color (by painting eggs) and continuity of incubation (by flushing parents from the nest at regular time intervals). In this study, I examined the value of cryptic egg coloration to mourning dove (Zenaida macroura) clutches under regimes of continuous versus interrupted incubation.

METHODS

Before beginning field work, I tested the effect of brown tempera paint on egg viability by measuring the evaporation rate of ring dove (Streptopelia risoria) eggs before and after they were spattered with paint. The laboratory results indicated that painting did not affect gas exchange.

Field work was done from May through early August 1983 at Big Creek State Park, Polk County, Iowa. The park contains several kilometers of windbreaks, most of which consisted of a multiflora rose (Rosa mutliflora) hedge flanked on one or both sides by double rows of jack pine (Pinus banksiana) or white pine (P. strobus). Most trees are less than 6 m tall, and land between windbreaks is either fallow or used to grow corn, alfalfa, or oats.

I found nests by walking within pine rows and flushing the parents. Immediately after a nest was discovered, I determined the age of eggs by candling (Hanson and Kossack 1963). In addition, several nest-site features were recorded: light intensity above the nest (measured with a light meter and expressed as a percentage of ambient light intensity), average nest visibility from 5 m away (subjectively evaluated on a scale of 1-4 [poor to excellent] from the four cardinal directions), height of vegetation above nest level (tree height minus nest height), nest support (sum of the diameters of all branches supporting the

nest), nest width, and depth of the nest bowl. Previous analyses indicated that these variables may influence nesting success (Westmoreland and Best 1985).

Each nest was randomly assigned to one of four treatments: (1) incubation interrupted and eggs cryptic, (2) incubation interrupted and eggs white, (3) incubation continuous and eggs cryptic, and (4) incubation continuous and eggs white. Immediately after a nest in treatments 1 or 3 was discovered, eggs were spattered with brown tempera paint to simulate cryptic coloration. To interrupt incubation in treatments 1 and 2, I flushed parents from each nest every 3 days until the nest failed or eggs hatched. I checked continuously incubated nests from about 5 m away (using binoculars) at the same interval, taking care not to approach so closely that the parent flushed. Nest checks in all treatments continued until the nest failed or the eggs hatched.

When a nest was found empty but intact, I attributed the failure to avian predators (Best and Stauffer 1980, and references therein). Mammalian (probably raccoons [Procyon lotor] and weasels) predation was assumed when the nest was torn apart or destroyed. Snakes and chipmunks (Tamias striatus) were rarely seen in the study area, so predation by them probably was rare. Small nocturnal mammals (mice and shrews) were not considered important predators because one mourning dove adult is present at the nest overnight.

Failures due to factors other than predation (i.e., wind blowing eggs from the nest or nest abandonment) were not included in the analyses.

Incubation was interrupted when nests were initially discovered. Thus, for continuously incubated nests (treatments 3 and 4), I eliminated from analysis all data on the interval between nest discovery and the subsequent visit. As a result, comparisons of nesting success between continuous and interrupted incubation regimes are biased and are not discussed here (but see Westmoreland and Best 1985). Comparing nesting success between cryptic versus white-egg clutches within each incubation regime, however, was valid. I calculated the daily nest survival probability (Mayfield 1975) for each treatment, and compared them by using one-tailed statistical tests (Hensler and Nichols 1981). Analyses of variance were used to test for differences in nest-site features among treatments.

RESULTS

I found 130 active nests. One failed due to high winds; 12 clutches with cryptic eggs and two clutches of white eggs were abandoned. Eleven of the cryptic-egg abandonments occurred immediately after the eggs were painted; only once did parents initially accept a modified clutch and abandon it later. McClure (1945) painted 10 mourning dove clutches various bright colors and observed the returning parents; all but one resumed incubation without hesitation. Seven of the cryptic-egg abandonments occurred at nests with interrupted incubation, and the remainder (5) at nests with continuous incubation.

Nest-site features and the age of eggs at nest discovery did not differ significantly ($P > 0.05$) among treatments (Table 1). This suggests that nesting success for treatments was not affected by factors other than egg color and incubation regime.

Cryptic coloration significantly ($P = 0.04$) reduced clutch losses when incubation was interrupted, but did not significantly influence clutch success when incubation was continuous (Table 2). Avian predators evidently caused 85% of the clutch failures, usually by removing eggs from nests. American Crows (Corvus brachyrhynchos) were seen frequently in the area and are known to carry dove-sized eggs away from nests when preying upon them (Montevecchi 1976b). Corvus

Table 1. Means of habitat variables and clutch age for each treatment^a

| Variable | <u>Incubation interrupted</u> | | <u>Incubation continuous</u> | |
|--|-------------------------------|-----------|------------------------------|-----------|
| | Cryptic | White | Cryptic | White |
| Vegetation height above nest level (m) | 2.1 ± 0.2 ^b | 2.2 ± 0.2 | 2.6 ± 0.5 | 2.5 ± 0.3 |
| Relative light intensity (%) | 21 ± 4 | 19 ± 3 | 14 ± 2 | 19 ± 2 |
| Nest concealment | 2.7 ± 0.2 | 2.8 ± 0.1 | 2.8 ± 0.2 | 2.7 ± 0.1 |
| Nest width (mm) | 116 ± 3 | 124 ± 2 | 120 ± 3 | 121 ± 4 |
| Nest-bowl depth (mm) | 14 ± 1 | 16 ± 1 | 17 ± 1 | 17 ± 1 |
| Nest support (mm) | 38 ± 7 | 44 ± 7 | 39 ± 5 | 46 ± 8 |
| Age (days) | 7.6 ± 1.2 | 5.9 ± 1 | 7.0 ± 1.3 | 5.7 ± 1.1 |

^aNo differences among treatments are significant.

^bStandard error.

Table 2. Nest success data for clutches of cryptic versus white eggs under different incubation regimes

| Treatment | # of nests | # of failures | Daily nest survival probability (\pm s.e.) | Estimated success ^a |
|------------------------|------------|---------------|---|--------------------------------|
| Incubation interrupted | | | | |
| Eggs cryptic | 29 | 8 | 0.957 ± 0.015 A ^b | 54% |
| Eggs white | 36 | 18 | 0.915 ± 0.019 B | 29% |
| Incubation continuous | | | | |
| Eggs cryptic | 19 | 2 | 0.980 ± 0.014 A | 75% |
| Eggs white | 31 | 7 | 0.958 ± 0.016 A | 55% |

^aBased on an incubation period of 14 days (see Mayfield 1975).

^bValues with the same letter within a group are not significantly different.

spp. were also the major predators in the experiments of Tinbergen et al. (1962) and Montevecchi (1976a).

DISCUSSION

My results suggest that cryptic egg coloration has strong adaptive value even when incubation is interrupted infrequently and for short periods. I attempted to determine return times for flushed adults, but was unable to find a method that did not cause abandonment or further increase the risk of predation. Casual observations, however, indicated that birds usually returned to the nest within 3 h. McClure (1945) recorded return times of 3-50 min and suggested that most returns are within 1 h.

I found no evidence of egg mortality caused by solar heating. My cryptically painted clutches were often exposed to incident radiation during adults' absences, but all eggs not taken by predators hatched normally.

One can imagine two scenarios in the coevolution of continuous incubation and white eggs in columbids: Eggs may have lost their color because constant incubation eliminated selection for crypticity, or columbids may have evolved constant incubation to cover their white eggs. I believe that the latter is more plausible. It seems likely that cryptic eggs probably would afford some selective value, even to continuously incubating columbids, when parents are flushed from the nest by predators. In my study, survival of cryptic eggs was greater than that for white eggs even when incubation was continuous. Although this difference was nonsignificant ($P = 0.15$, Table 2), the hypothesis that

cryptic egg coloration is valuable to continuously incubating columbids should not be rejected because the power of the test is low (0.37, calculated by James D. Nichols, Patuxent Wildlife Research Station, Patuxent, Maryland).

White eggs may indicate that columbids evolved from cavity nesters (see discussion in Goodwin 1983). And some aspects of columbid incubation behavior suggest that continuous incubation evolved, at least partially, as a mechanism to reduce the conspicuousness of white eggs. When approached, incubating mourning doves crouch on the nest and do not flush until almost in contact with the intruder (Laub 1956, Walsberg and Voss-Roberts 1983). Brightly colored, male purple-crowned pigeons (Ducula spilorrhoa) also remain on the nest when approached, but they shift positions to keep a patch of cryptic undertail feathers oriented toward intruders (Crome 1975a). Behavioral egg concealment also occurs in noncolumbid open-nesting birds with white eggs. Several ground-nesting species of ducks, geese, grebes, and gallinaceous birds cover their eggs with down or vegetation when leaving the nest (Welty 1982).

GENERAL CONCLUSION

The unusual reproductive traits of mourning doves interact to produce a successful reproductive strategy based on multiple brooding. Mourning doves have long breeding seasons because they produce crop milk in vivo and feed older nestlings a diverse diet of seeds, thus allowing time for production of numerous broods. Most other birds have to synchronize reproduction with a brief period of food abundance (Lack 1950, Skutch 1950, Thompson 1950). Other adaptations in columbids serve to increase the number of nesting cycles per season by shortening the nesting cycle or minimizing the interval between successive nesting attempts.

On average, columbid nesting cycles are 22% shorter than those of other altricial land birds. Constant incubation, small clutch size, fast nestling growth, and early fledging all contribute to minimizing the length of the nesting cycle. Constant incubation also eliminates the need for incubation patches in adults, and minimizes the negative effect of conspicuous egg coloration. Mourning doves are capable of incubating three eggs and raising three offspring, but prolonged nestling periods and low post-fledging survival probably negate any selective advantage to doing so. Predation as a selective force augments the advantage of short nesting cycles.

To minimize the interval between nesting attempts, mourning doves construct small nests and reuse old nests.

This allows them to initiate nesting cycles quickly, despite their ritualized building behavior. In addition, small clutch size and a lesser role in crop-milk production may allow females to initiate new clutches quickly, and sometimes to overlap nesting cycles.

LITERATURE CITED

- Ackerman, R. A., and R. C. Seagrave. 1984. Parent-egg interactions: egg temperature and water loss. Pp. 73-88. In G. C. Whittow and H. Rahn, Eds. Seabird energetics. Plenum, New York.
- Alison, R. M. 1976. Mourning doves wintering in Ontario. Can. Field-Nat. 90:174-176.
- Bakken, G. S., V. C. Vanderbilt, W. A. Buttemer, and W. R. Dawson. 1978. Avian eggs: thermoregulatory value of very high near-infrared reflectance. Science 200:321-323.
- Bartholomew, G. A. 1972. Body temperature and energy metabolism. Pp. 298-368. In M. S. Gordon, Ed. Animal physiology: principles and adaptations. Macmillan, New York.
- Bates, R. W., E. L. Lahr, and O. Riddle. 1935. The gross action of prolactin and follicle-stimulating hormone on the mature ovary and sex accessories of the fowl. Am. J. Physiol. 111:361-368.
- Bates, R. W., O. Riddle, and E. L. Lahr. 1937. The mechanism of the anti-gonad action of prolactin in adult Pigeons. Am. J. Physiol. 119:610-614.
- Bertram, B. C. R., and A. E. Burger. 1981. Are ostrich Struthio camelus eggs the wrong colour? Ibis 123:207-210.
- Best, L. B., and D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. Condor 82:149-158.
- Blockstein, D. E. 1982. Nesting behavior of mourning doves (Zenaida macroura) in Minnesota. Unpublished M.S. thesis. Univ. Minnesota, Minneapolis.
- Boersma, P. D., and N. T. Wheelwright. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the fork-tailed storm petrel. Condor 81:157-165.
- Breitenbach, R. P., and T. S. Baskett. 1967. Ontogeny of thermoregulation in the mourning dove. Physiol. Zool. 40:207-217.
- Brisbin, I. L., Jr. 1969. Bioenergetics of the breeding cycle of the ring dove. Auk 86:54-74.

- Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.* 109:677-699.
- Browning, B. M. 1959. An ecological study of the food habits of the mourning dove. *California Fish and Game* 45:313-331.
- Burley, N. 1980. Clutch overlap and clutch size: alternative and complementary reproductive tactics. *Am. Nat.* 115:223-246.
- Caldwell, L. D. 1964. Dove production and nest site selection in southern Michigan. *J. Wildl. Mgmt.* 28:732-738.
- Charnov, E. L., and J. R. Krebs. 1974. On clutch-size and fitness. *Ibis* 116:217-219.
- Cheng, M. F., and J. Balthazart. 1982. The role of nest-building activity in gonadotrophin secretions and the reproductive success of ring doves (*Streptopelia risoria*). *J. Comp. Physiol. Psychol.* 96:307-324.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* 20:174-184.
- Coon, R. A., J. D. Nichols, and H. F. Percival. 1981. Importance of structural stability to success of mourning dove nests. *Auk* 98:389-391.
- Cottam, C., and J. B. Trefethen. 1968. *Whitewings*. D. Van Nostrand, Princeton.
- Cowan, J. B. 1952. Life history and productivity of a population of western mourning doves in California. *California Fish and Game* 38:505-521.
- Crome, F. J. H. 1975a. Notes on the breeding of the purple-crowned pigeon. *Emu* 75:172-174.
- Crome, F. J. H. 1975b. Breeding, feeding and status of the Torres Strait pigeon at Low Isles, North-eastern Queensland. *Emu* 75:189-198.
- Crossner, K. A. 1977. Natural selection and clutch size in the European starling. *Ecology* 58:885-892.
- Delacour, J. 1980. *Wild pigeons and doves*. T. F. H. Publications, Neptune, New Jersey.

- Drent, R. H. 1972. The natural history of incubation. Pp. 262-322. In D. S. Farner, Ed. Breeding biology of birds. Natl. Acad. Sci., Washington.
- Drent, R. H. 1975. Incubation. Pp. 333-419. In D. S. Farner and J. R. King, Eds. Avian biology. Vol. V. Academic Press, New York.
- Foster, M. S. 1974. A model for molt-breeding overlap and clutch size in some tropical birds. *Evolution* 28:182-190.
- Frith, F. H. J. 1982. Pigeons and doves of Australia. Rigby, Sydney.
- Galant, A. R. 1975. Nonlinear regression. *Am. Stat.* 29:73-81.
- Gaston, A. J. 1985. Energy invested in reproduction by thick-billed murres (Uria lomvia). *Auk* 102:447-458.
- Gibbons, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart and Winston, New York.
- Goforth, W. R., and T. S. Baskett. 1971. Social organization of penned mourning doves. *Auk* 88:528-542.
- Goodwin, D. 1983. Pigeons and doves of the world. 3rd ed. Cornell Univ. Press, Ithaca, New York.
- Grand, J. B., R. R. Hitchcock, and R. E. Mirarchi. 1984. Mortality of nestling and fledgling mourning doves in east central Alabama. *J. Alabama Acad. Sci.* 55:131.
- Grant, P. R., and K. T. Grant. 1979. Breeding and feeding ecology of the Galapagos dove. *Condor* 81:397-403.
- Greenlaw, J. S. 1978. The relation of breeding schedule and clutch size to food supply in the rufous-sided towhee. *Condor* 80:24-33.
- Gutierrez, R. J., C. E. Braun, and T. P. Zapatka. 1975. Reproductive biology of the band-tailed pigeon in Colorado and New Mexico. *Auk* 92:665-677.
- Haas, G. H. 1980. Success of single-parent mourning dove nests. *Proc. Ann. Conf. Southeastern Assoc. Fish and Wildl. Agencies* 34:426-429.
- Hanson, H. C., and C. W. Kossack. 1963. The mourning dove in Illinois. Illinois Dept. Conserv. Tech. Bull. No. 2, Springfield.

- Harris, M. P. 1970. Breeding ecology of the swallow-tailed gull, Creagrus furcatus. Auk 87:215-243.
- Harris, S. W., M. A. Morse, and W. H. Longley. 1963. Nesting and production of the mourning dove in Minnesota. Am. Midl. Nat. 69:150-172.
- Harrison, C. 1978. A field guide to the nests, eggs, and nestlings of North American birds. Collins, New York.
- Haverschmidt, F. 1953. Notes on the life history of Columbigallina talpacoti in Surinam. Condor 55:21-25.
- Haymes, G. T., and R. D. Morris. 1977. Brood size manipulations in herring gulls. Canadian J. Zool. 55:1762-1766.
- Helwig, J. T., and K. A. Council. 1979. SAS user's guide. SAS Institute, Inc., Raleigh, N.C.
- Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93:42-53.
- Hitchcock, R. R., and R. E. Mirarchi. 1984. Duration of dependence of wild fledgling mourning doves upon parental care. J. Wildl. Mgmt. 48:99-108.
- Johnson, R. F. 1960. Behavior of the Inca dove. Condor 62:7-24.
- Jones, R. E. 1971. The incubation patch of birds. Biol. Rev. 46:315-339.
- Keeler, J. E., Chr. 1977. Mourning dove (Zenaida macroura). Pp. 275-298. In G. C. Sanderson, Ed. Management of migratory shore and upland game birds in North America. Univ. Nebraska Press, Lincoln.
- Kendeigh, S. C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. 22:1-356.
- King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4-85. In R. A. Paynter, Jr., Ed. Avian energetics. Publ. Nuttall Ornithol. Club No. 15.
- Koepcke, M. 1972. Uber die resistenzformen der vogelnester in einem begrenzten gebiet des tropischen regenwaldes in Peru. J. Ornithol. 113:138-160.

- Kruijt, J. P. 1958. Speckling of the herring gull egg in relation to breeding behavior. Arch. Neerl. Zool. 12:565-567.
- Lack, D. 1947. The significance of clutch size. I,II. Ibis 89:302-352.
- Lack, D. 1948. The significance of clutch-size. Part III. Some interspecific comparisons. Ibis 90:25-45.
- Lack, D. 1950. The breeding seasons of European birds. Ibis 92:288-316.
- Lack, D. 1958. The significance of the colour of turdine eggs. Ibis 100:145-166.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, London.
- Laub, W. K. 1956. The relation of parental care and the condition of the glandular crop to the successful rearing of young mourning doves, Zenaidura macroura (L.). Unpublished M.S. thesis. Ohio State Univ., Columbus.
- Levi, W. M. 1963. The pigeon. R. L. Bryan Co., Columbia, South Carolina.
- Lloyd, C. S. 1977. The ability of the razorbill Alca torda to raise an additional chick to fledging. Ornis Scand. 8:155-159.
- Lumpkin, S., K. Kessel, P. G. Zenone, and C. J. Erickson. 1982. Proximity between the sexes in ring doves: social bonds or surveillance? Anim. Behav. 30:506-513.
- MacGregor, W. G., and W. M. Smith. 1955. Nesting and reproduction of the band-tailed pigeon in California. California Fish and Game 41:315-326.
- Mackey, J. P. 1954. Some aspects of mourning dove behavior related to reproduction. Unpublished M.S. thesis. Ohio State Univ., Columbus.
- Mackey, J. P. 1965. Cooing frequency and permanence of pairing of mourning doves. J. Wildl. Mgmt. 29:824-829.
- Maridon, B. and L. C. Holcomb. 1971. No evidence for incubation patch changes in mourning doves throughout reproduction. Condor 73:374-375.

- Mayfield, H. F. 1975. Suggestions for calculating nesting success. *Wilson Bull.* 87:456-466.
- McClure, H. E. 1941. Ecology and management of the mourning dove, Zenaidura macroura (Linn.), in southwest Iowa. Ph.D. dissertation. Iowa State Univ., Ames.
- McClure, H. E. 1945. The reaction of the mourning dove to colored eggs. *Auk* 62:270-272.
- McClure, H. E. 1950. An eleven-year summary of mourning dove observations in the west. *Trans. North Amer. Wildl. Conf.* 15:335-346.
- McGillivray, W. B. 1983. Intraseasonal reproductive costs for the house sparrow (Passer domesticus). *Auk* 100:25-32.
- Mirarchi, R. E., and P. F. Scanlon. 1983. Duration of mourning dove crop gland activity during the nesting cycle. *J. Wildl. Mgmt.* 44:209-213.
- Montevecchi, W. A. 1976a. Field experiments on the adaptive significance of avian eggshell pigmentation. *Behaviour* 58:26-39.
- Montevecchi, W. A. 1976b. Egg size and the egg predatory behaviour of crows. *Behaviour* 57:307-320.
- Morse, D. H. 1975. Mourning doves breeding in an unusual habitat: the coastal spruce forest. *Wilson Bull.* 87:422-424.
- Murton, R. K., and A. J. Isaacson. 1962. The functional basis of some behaviour in the woodpigeon Columba palumbus. *Ibis* 104:503-521.
- Murton, R. K., A. J. Isaacson, and N. J. Westwood. 1963. The food and growth of nestling wood-pigeons in relation to the breeding season. *Proc. Zool. Soc. London* 141:747-781.
- Murton, R. K., N. J. Westwood, and A. J. Isaacson. 1974. Factors affecting egg-weight, body-weight and moult of the woodpigeon, Columba palumbus. *Ibis* 116:52-73.
- Needham, J. 1942. *Biochemistry and morphogenesis*. Cambridge Univ. Press, Cambridge.
- Nice, M. M. 1922. A study of the nesting of mourning doves. *Auk* 39:457-474.

- Pace, D. M., P. A. Landolt, and F. E. Mussehl. 1952. The effect of pigeon crop-milk on growth in chickens. *Growth* 16:279-285.
- Parmelee, D. F., and R. B. Payne. 1973. On multiple broods and the breeding strategy of arctic sanderlings. *Ibis* 115:218-226.
- Peters, H. S. 1961. The past status and management of the mourning dove. *Trans. North Am. Wildl. Nat. Resource Conf.* 26:371-374.
- Plumb, W. J. 1965. Observations on the breeding biology of the razorbill. *British Birds* 58:449-456.
- Rahn, H., and A. Ar. 1974. The avian egg: incubation time and water loss. *Condor* 76:147-152.
- Rahn, H., C. V. Paganelli, and A. Ar. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.
- Rana, B. D. 1975. Breeding biology of the Indian ring dove in the Rajasthan desert. *Auk* 92:322-332.
- Ricklefs, R. E. 1968a. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. *Proc. Natl. Acad. Sci.* 61:847-851.
- Ricklefs, R. E. 1968b. Patterns of growth in birds. *Ibis* 110:419-451.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* No. 9.
- Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292. In R. A. Paynter, Ed. *Avian energetics*. Publ. Nuttall Ornithol. Club No. 15.
- Ricklefs, R. E. 1984. The optimization of growth rate in altricial birds. *Ecology* 65:1602-1616.
- Russell, S. M. 1969. Regulation of egg temperatures by incubating white-winged doves. Pp. 107-112. In C. C. Hoff and M. L. Riedesel, Eds. *Physiological systems in semiarid environments*. Univ. New Mexico Press, Albuquerque.
- Saari, L. 1979. On the breeding biology of the wood pigeon (*Columba palumbus*) in Finland. *Finnish Game and Fish. Res. Inst.*, Helsinki.
- Safriel, U. N. 1975. On the significance of clutch size in

nidifugous birds. Ecology 56:703-708.

- Sayre, M. W., T. S. Baskett, and K. C. Sadler. 1980. Radiotelemetry studies of the mourning dove in Missouri. Missouri Dept. Conservation Terrestrial Ser. No. 9, Jefferson City.
- Scanlon, P. F., J. E. Clarke, C. J. Flick, and W. H. Taylor. 1981. Aspects of mourning dove nesting in Virginia. Virginia J. Sci. 32:97.
- Schorger, A. W. 1955. The passenger pigeon: its natural history and extinction. Univ. Wisconsin Press, Madison.
- Skutch, A. F. 1950. The nesting seasons of Central American birds in relation to climate and food supply. Ibis 92:185-222.
- Skutch, A. F. 1962. The constancy of incubation. Wilson Bull. 74:115-152.
- Spencer, A. W., and H. W. Steinhoff. 1968. An explanation of geographic variation in litter size. J. Mammal. 49:281-286.
- Swank, W. G. 1955. Nesting and production of the mourning dove in Texas. Ecology 36:495-505.
- Taylor, M. H. 1941. Breeding and nesting activities of the eastern mourning dove in North Carolina. Unpublished M.S. thesis. North Carolina State Univ., Raleigh.
- Thompson, A. L. 1950. Factors determining the breeding seasons of birds: an introductory review. Ibis 92:173-184.
- Tinbergen, N., G. J. Broekhuysen, F. Feekes, J. C. W. Houghton, H. Kruuk, and E. Szulc. 1962. Egg shell removal by the black-headed gull, Larus ridibundus L.; a behaviour component of camouflage. Behaviour 19:74-117.
- Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. Am. Nat. 103:501-516.
- Utter, J. M., and E. A. Lefebvre. 1973. Daily energy expenditure of purple martins (Progne subis) during the breeding season: estimates using D₂O¹⁸ and time-budget methods. Ecology 54:597-603.
- Vermeer, K. 1963. The breeding ecology of the glaucous-winged gull (Larus glaucescens) on Mandarte

Island, B.C. Occas. Pap., Brit. Columbia Prov. Mus.
Nat. Hist. Anthropol. 13:1-104.

Walsberg, G. E., and K. A. Voss-Roberts. 1983. Incubation
in desert-nesting doves: mechanisms for egg cooling.
Physiol. Zool. 56:88-93.

Weeks, H. P. 1980. Unusual egg deposition in mourning
doves. Wilson Bull. 92:258-260.

Welty, J. C. 1982. The life of birds. Saunders, New York.

Westmoreland, D., and L. B. Best. 1985. Effects of
researcher disturbance on mourning dove nesting success.
Auk 102:774-780.

Woolfenden, G. E., and S. A. Rohwer. 1969. Breeding birds
in a Florida suburb. Bull. Florida State Mus. 13:1-83.

Zimmerman, J. L. 1983. Cowbird parasitism of dickcissels in
different habitats and at different nest densities.
Wilson Bull. 95:7-22.

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